

MATING FREQUENCIES OF MALE CRAB SPIDERS, *MISUMENA VATIA* (ARANEAE, THOMISIDAE)

Douglass H. Morse: Department of Ecology & Evolutionary Biology, Box G-W,
Brown University, Providence, Rhode Island 02912 USA.
E-mail: d_morse@brown.edu

ABSTRACT. The number of matings obtained by a male is likely to be a major component of his lifetime fitness. Males that depend on finding mates before their competitors must allocate resources to this effort, potentially at the expense of their reproductive rate. Male crab spiders *Misumena vatia* (Clerck 1757) often occur at low densities and experience considerable difficulty in finding females. This constraint might select for their cursorial body form and high movement rates at the expense of their reproductive rate. Male *M. vatia* will not mate more than once in rapid succession and typically no more than once every other day, although they are capable of several matings over their lifetime. Males may rarely encounter virgin females more often than once every other day and thus would experience little loss of fitness from an inability to mate in rapid order.

Keywords: Male fitness, reproductive constraint, scramble competition

The key determinant of male lifetime fitness often is the number of matings a male obtains (Williams 1992). Under many circumstances the difference in number of matings among males is high, reaching its maximum in harem formers, and variance in male fitness is generally taken to be higher than that of females, a consequence of differences between the sexes in investment per offspring. In high-density situations, males may achieve such variance via a dominance hierarchy, which often is size-related (LeBouef 1974; Clutton-Brock et al. 1982). Low-density situations in which male-male contact is the exception provide a situation in which different factors dictate success; here, the first male to find a female may instead be the one to succeed via scramble competition, accompanied by first-male sperm priority (Ghiselin 1974; LeGrand & Morse 2000).

A male should normally maximize the situations in which he can capitalize upon a reproductive opportunity. However, factors other than the ability to mate successively may assume importance. For instance, males that must expend considerable energy and time in finding females may be unable to mate repeatedly, but seldom find themselves in a situation where that ability would provide an advantage. If so, extra allocation to effective movement, even at the expense of failing to

mate females in rapid succession, would provide important benefits at a likely infrequent cost.

Adult male spiders are often assumed to be less common than their females (Foelix 1996), primarily because of an assumed disproportionately high mortality incurred from searching for females (Vollrath & Parker 1992; Shuster & Wade 2003). However, females of many species do not mature simultaneously, with the result that overt competition may nevertheless occur for access to females as they molt into their adult stage, with consequent guarding of penultimate females in many instances. In spite of potential competition, populations with a low number of males relative to females present the opportunity for males, on average, to mate several times.

My crab spider *Misumena vatia* (Clerck 1757) populations exhibit a female-biased primary sex ratio (1.5 females to 1 male), and this ratio shifts to 2.5–5.1 females to 1 male by the adult stage (LeGrand & Morse 2000). Further, adults are not abundant (Holdsworth & Morse 2000) and the males experience considerable difficulty in finding females, which apparently do not emit pheromonal cues (Anderson & Morse 2001; Leonard & Morse 2006), as opposed to other spider species examined in this regard (Tietjen 1977; Elgar &

Schneider 2004). Given this combination of traits, male *M. vatia* should experience strong selection to reproduce multiple times, but the ability to mate in rapid succession would not be under equally strong selection. The number of matings by individual males in my populations is open to question; nevertheless, adult males on average must mate several times in their lifetime, a consequence of the sex ratios of adults noted above (LeGrand & Morse 2000), the extremely high proportion of adult females that produce fertile egg masses (Morse 1994), and the lack of any evidence to suggest that *M. vatia* ever reproduces parthenogenetically (D. H. Morse, unpublished data). The purpose of this study is to establish whether male *M. vatia* will mate in rapid succession and if not, with what frequency they do successfully mate. The results will provide insight into the evolution of this breeding system.

METHODS

Spiders were collected from flowers in fields and along roadsides in South Bristol, Lincoln County, Maine, USA (43.96°N, 69.56°W) during June 1998–2006 and subsequently maintained in 7-dram vials (~26 ml; 5 cm long × 3 cm diameter) until testing. They were fed small moths and flies every other day. All females were collected as penultimates and used as adults within a week after their final molt. Males were collected either as penultimates or adults. Adult males were not mated for the first two days after collection. In all but one experiment individuals were tested within the first week after capture, or the first week after final molt in the case of the penultimates, to insure that their behavior matched that of individuals in the field (Leonard & Morse 2006). In the single exception I repeatedly paired nine males over periods as long as two months to establish how many times they would mate. Matings of *M. vatia* are described in detail in Morse (2007).

To test the ability of an adult male to mate more than once in succession, I first presented him with a recently molted virgin adult female perched on an ox-eye daisy *Chrysanthemum leucanthemum* flower, a frequent hunting site at the time that females molt into the adult stage. Female *M. vatia* readily mate as soon as they have completed their final molt

(Holdsworth & Morse 2000). Five minutes after positioning the female, I released the male onto the flower stem immediately below the flower. Since males almost inevitably move upward in this circumstance (Hu & Morse 2004), they are well positioned to find the female. I observed the male for 30 min after he climbed into the flower, or until he mated with the female. Previous experiments have demonstrated that males not mating within 30 min are unlikely to do so subsequently (Hu & Morse 2004). I ran 28 male-female pairs in this way. Matings usually took 3–10 min, and the males then quickly dismounted the females and retreated a minimum of several body lengths from them (Hu & Morse 2004).

Following these initial runs I presented 14 of the successful males with a second virgin female to determine if they would mate twice in succession. As before I placed the female on a fresh daisy and released the male on the stem of this flower five min later. All second presentations were made within 10 min of the termination of the initial mating.

Any females that these males refused to mate in the first run were then paired with other males that had not mated within the past two days. Any of these males that did not mate with the female presented them in the first run were tested in the same way with a second virgin female, and if they mated with the second female, they were then paired with a third virgin female. Thus all males were given the opportunity to mate twice in succession, and all females that did not mate in their first run were given the opportunity to mate with a second male.

I also further investigated how frequently and how many times males would mate over their adult lifetime. To test frequency, I ran 10 males in the same way as noted above and then repeated the procedure on the following day. I also mated nine other males with virgin females at two-day intervals five to 20 times. Voucher specimens of *Misumena vatia* have been deposited in the American Museum of Natural History, New York.

RESULTS

Twenty-three of 28 males (82.1%) mated with the first virgin female presented them within the 30 min period. All the males that mated inserted both pedipalps one or more times. Of the remaining males, one individual

had still not contacted the female after 30 min, and the remaining four contacted the female but did not mate.

When 14 of the males that mated with the first female were presented with a second virgin female, none of these males would mate with the second females. The difference in their performance in the first and second runs is highly significant (one-tailed sign test, $P < 0.001$). The 14 females used for these second matings were then tested with a new set of adult males. These males mated with all 14 of the females. The performance of the two groups of males with this set of females was highly significantly different ($P < 0.001$, same test).

Four of the five males that did not mate with the first virgin female presented to them proceeded to mate with another virgin female presented to them immediately after the first one, but all five of them refused to mate with a third virgin female that was presented immediately after their second run. The five initially rejected females were eschewed by a subsequent set of males as well, but these last males mated with another set of virgin females presented to them.

All 10 males tested on successive days failed to mate with virgin females on the following day. When I subsequently tested another set of males ($n = 9$) every other day, they mated in 82.5% of the pairings with virgin females (5–20 matings per male, 80 individual runs, 73.7–90.9% acceptance rate), significantly different from the results on successive days ($P < 0.001$ in a Mann-Whitney U -test for independent samples). Since males refused to mate on successive days but usually mated every other day, I conclude that they require a two-day interval between matings.

DISCUSSION

Clearly these male *M. vatia* will not mate twice in rapid succession, or on successive days (but see below), although they will routinely mate every other day. I did not attempt to test them at various intervals between one and two days, but since they are usually diurnal (Morse 1981), even if they could mate at, say, 1.5-day intervals, they would be unlikely to do so in the field.

The second females presented to the males were apparently in no way deficient as mates, so I conclude that the failure of the first set

of males to mate with them resulted from the males' inability to mate twice in rapid succession. The females eschewed by the males in this first test were for some unknown reason unacceptable to all males tested, but the third set of females were likely eschewed by the latter males only because of their apparent inability to mate twice in rapid succession. Thus, the four males that eschewed the first female but mated with the second one should probably be treated as performers rather than nonperformers in this analysis; that is, they mated when presented with the first acceptable female. If so, this correction would change the proportion of male performers to 96.4% (27 of 28).

Mate-choice theory suggests that males should be choosy if presented with an excess of females (see Andersson 1994). Since the average male *M. vatia* in these populations reproduces several times in his lifetime (LeGrand & Morse 2000), one might predict a tendency for choosiness, especially since they do not mate in rapid succession. However, the tendency for males to mate with any available virgin female after a sufficient hiatus bolsters the argument that they do not frequently meet adult virgin females.

The failure to mate in rapid succession would be counterproductive if the males encountered more than one virgin female within a brief period of time. The low population density of these spiders (LeGrand & Morse 2000), combined with the failure of the females to molt simultaneously or to advertise their condition (Anderson & Morse 2001; Leonard & Morse 2006), makes it further unlikely that the failure to mate in rapid sequence constitutes a significant constraint for the males. The average female in this population was not mated until approximately 1.5 days after molting into the adult stage (LeGrand & Morse 2000), although females will readily mate immediately after their last molt (Holdsworth & Morse 2000). Males capable of mating on an every-other-day basis should thus easily account for insemination of all of the females in the population (Morse 1994). However, at this point I do not know whether mating slows a male's subsequent searching rate, nor whether such a slowdown would significantly affect the frequency with which it finds a new female. I also do not know wheth-

er a male needs to recharge his palps before mating a second time.

In spite of the attention paid to the reproductive behavior of spiders, relatively little is known about either the frequency with which males recharge their pedipalps or the mating rates of species that can mate several times. The effect of sperm depletion for multiply mating males is rarely explicitly considered in the literature (Jones et al. 2006). Quantitative data on rates of pedipalp recharging and mating frequencies of spiders appear to be non-existent. Neither subject is discussed in standard treatises on spider biology such as Savory (1928), Bristowe (1958), Gertsch (1979) and Foelix (1996), though Gertsch (1979) notes without attribution that some species can mate multiple times without recharging their pedipalps, while others have to recharge during mating. Most recent attention to mating rates of male spiders focuses on extreme adaptations in which a male is physiologically or anatomically incapable of mating more than once or twice in its lifetime (e.g., *Tidarren argo*, Theridiidae: Knoflach & van Harten 2001; *Lacrodectus hasselti*, Theridiidae: Andrade and Kasumovic 2005; *Argiope keyserlingi*, Araneidae: Herberstein et al. 2005).

Although it is possible that males failed to mate in rapid succession because they did not have time to recharge their pedipalps with sperm during the experimental period, several lines of evidence suggest that this factor does not explain the failure of these males to mate with a second female in the experiments. First, males almost inevitably refuse to mate again on the day following a mating (no observations in this study and only rare instances in other observations: D. H. Morse pers. obs.). Second, I observed no efforts by the spiders to recharge their pedipalps shortly following a mating in this study. Finally, the males inserted their pedipalps into the females' genital apertures a variable number of times during a mating sequence, so it is unclear whether the males always used up their supply of sperm in the pedipalps. I did not measure sperm loads in the pedipalps because of the limited number of males available for experimentation and their multiple use in these and other experiments.

In addition to the data gathered specifically for this study, I have made it a policy to mate

virgin females used for other studies with males that have not mated the previous day, because I have so seldom obtained matings with males that mated the previous day (D. H. Morse unpubl. data). The males that I ran the largest number of times usually mated on alternate days as long as we could find virgin females for them. Several of these matings produced viable clutches, though in other circumstances I was unable to rear the females to their egg-laying stage before the season ended (D. H. Morse unpubl. data).

It must be reiterated that these males were confined, so that their responses may differ somewhat from individuals in the field. However, I attempted to minimize this effect by testing individuals soon after collecting them. With the exception of the males run multiple times, all males were run within a week of their capture, a period during which confined individuals perform several other acts [foraging (Morse 2000, 2005), line running (Leonard & Morse 2006), orientation and activity (Sullivan & Morse 2004)] similarly to unrestrained individuals in the field.

These males thus form an extreme opposite pole to harem formers (Andersson 1994), although many of them also mate several times under natural circumstances. Harem formers exhibit some of the most extreme examples of sexual dimorphism favoring large males, but these crab spiders are among the most extreme examples of sexual dimorphism favoring small males; although both exhibit a female-biased sex ratio at reproduction (Morse 2007).

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